

# EXPERIMENTAL INVESTIGATIONS ON BIRCH AND OAK<sup>1</sup>

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(WITH PLATES XII-XV AND FOUR FIGURES)

At the present time experimental investigations have a well merited vogue, especially in genetical and morphological fields. Until recently, however, little has been done in this connection on the structure of woody plants. This has been due largely to the fact that the history of woody plants has not been sufficiently understood to warrant their interpretation. The doctrine of evolution was formulated mainly through the study of comparative anatomy in the absence of a fossil record. Plant tissues, however, are more resistant to decay than animal tissues (with the exception of bones), and as a consequence their historical relations and affinities have become available for comparison with existing forms and structures. The comparative anatomical study of existing and fossil plants has led to the conclusion that there are certain general principles which not only hold true for a group of plants in which there is a fossil record, but also may be applied to other groups in which, as in the Angiosperms, there is as yet no complete geological record. Certain general conclusions thus inductively established make it possible to apply the same principles in judging anatomical features and interpreting structural relationships in the Angiosperms, in absence of fossil record (4, 5, 7).

The first principle established as a result of comparative anatomical study and knowledge of fossil forms, and one employed by zoölogists, is based on the fact that in the course of their development organisms may pass through conditions now lost in adult life, but once possessed by the organism in its mature state. This is called the law of recapitulation, and holds true in plants also. For example, certain of the Cupressineae which have small leaves in the adult plant, in their seedling development have the larger leaves characteristic of the more ancient flora.

<sup>1</sup> Contribution from the Laboratories of Plant Morphology of Harvard University.

A comparative anatomical study of existing and fossil plants, especially the Gymnosperms, has shown that certain parts of plants (as the root, leaf, first annual ring, and reproductive axis) may have a different organization of tissues from the stem, which is more highly specialized. This fact has been responsible for the theory of retention, or, as it has been more recently called, the doctrine of conservative organs (7).

The third principle is based on the fact that upon injury certain structures and types of organization appear which are characteristic of older forms and more conservative regions of the plant. It is less well understood than the other two, and is capable of more misinterpretation. It is the one of chief interest in the present investigation. It should be pointed out, however, that only those structures occurring as a result of wounding which are comparable to conditions presented by the seedling and the conservative organs (root, leaf, etc.) can be relied upon in the interpretation of wound reactions.

Experimental work on woody tissues is of interest not only from a general biological standpoint, but is also of importance from the point of view of plant pathology. It may be pointed out also that such investigations are of interest from an economic point of view, since they suggest the possibility of producing experimentally valuable ornamental woods.

As the subject of wound reactions is a large and complicated one, for the purposes of brevity and clearness I have confined myself to those traumatic features which are connected with ray structures only. Other reversions and reactions consequent upon injury in the birch and oak, therefore, may be conveniently postponed until a later date.

### Ray organization in Angiosperms

The three types of broad rays characteristic of the angiospermous forest trees are all found in different species of the isolated and probably ancient genus *Casuarina*. A synoptic diagram illustrating these types as seen in *Casuarina* is given in text fig. 1. The simple or uniseriate ray which is a feature of the wood organization of the Conifers is also found in Angiosperms, and its occurrence

need only be noted in the present connection. In the center of text fig. 1 is the type of ray known as the aggregate ray ( $A, A'$ ). This is a radial band composed of congeries of small or uniseriate rays and clusters of fibers. The leaf trace is represented in solid black at the interior of the segment. The aggregate ray originated probably in the clustering of uniseriate rays around the outgoing leaf trace, and seems to be the most ancient type of broad ray found in forest trees. It is found in the root and seedling stem of

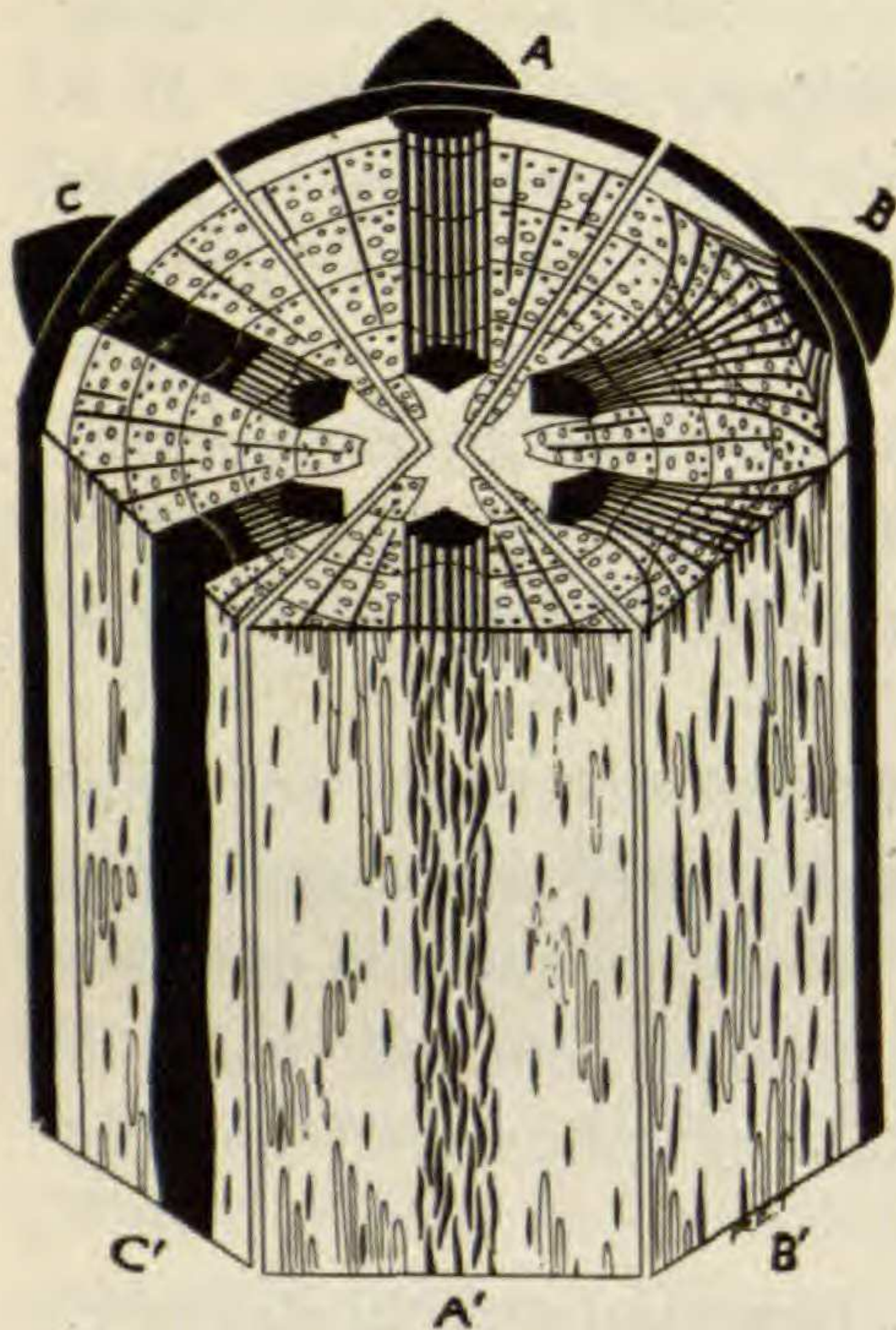


FIG. 1

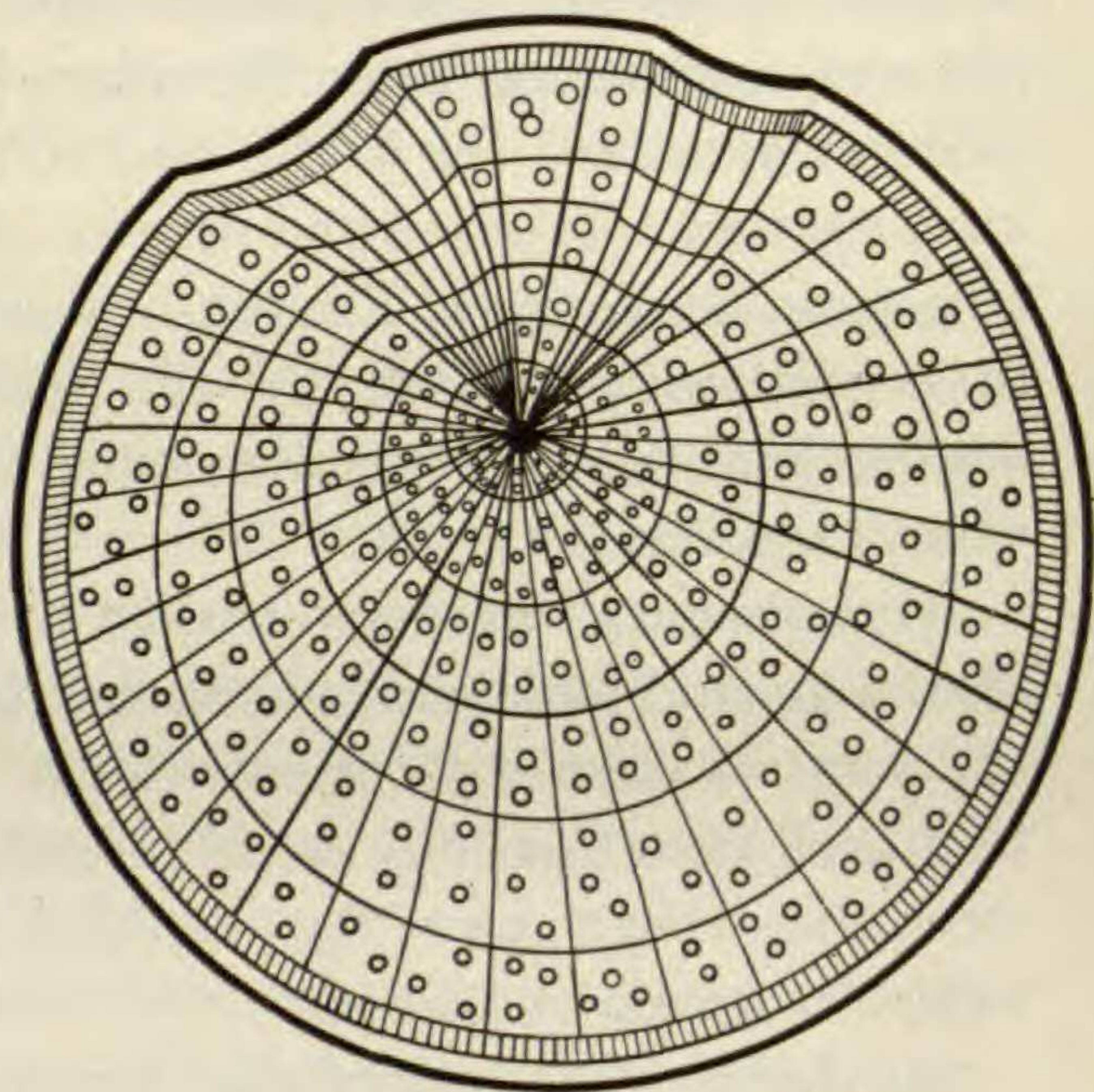


FIG. 2

FIGS. 1, 2.—Fig. 1, synoptic diagram illustrating ray situation in *Casuarina*; fig. 2, diagram of birch root.

*Casuarina*, and persists in the adult axis of *C. torulosa*. It is also characteristic of the adult stem wood of the alder and of the southern oaks.

The second type of angiospermous ray, represented at the left of the diagram, is known as the compound ray. It is found in *Casuarina Fraseri*, in the mature axes of oaks of northern range, and in herbaceous Dicotyledons. Immediately outside of and subtending the leaf trace (black) is the aggregate condition already mentioned. Farther out toward the periphery of the stele, however, the fibrous parts of the ray have undergone a parenchymatous

metamorphosis. The homogeneous character of the ray is indicated by solid black. The depressions of the cylinder, corresponding in position to the large rays in the vicinity of the annual ring, are to be noted.

The type of ray characteristic of the majority of our forest trees is the diffuse ray. The organization of this is shown at the right (*B, B'*). Just outside the leaf trace (black) the ray is characteristically aggregate, a situation parallel to that of the early organization of the compound ray. Farther out, however, the rays spread out and subdivide, instead of being more closely united, and vessels and fibers again appear in the foliar segment. This permits the passage of more water and food substance, and is of advantage to trees subject to the rigors of a northern winter. In tangential aspect the rays are several cells wide, which differentiates them from the simple or uniseriate rays of the Conifers. This type of ray is found in the mature stem of *C. stricta* and *C. equisetifolia*.

#### Ray organization in birch and oak

BIRCH.—Fig. 1 represents a transverse section through the stem wood of *Betula nigra*, and shows the type of ray characteristic of most of our forest trees. Fig. 2 shows some of these diffuse rays in tangential aspect. They are about three or four cells in width, but without any interspersed fibers. It is an interesting fact that most birches of southern origin or affinity retain the aggregate type of ray organization in their vegetative axes, while those of northern range are characterized by the diffuse type of ray. \**B. populifolia*, for instance, which is essentially a southern birch, has persistent aggregate rays in the normal stem wood. *B. pumila* and *B. lutea* may be taken as examples of the northern species. This difference in ray organization would seem to indicate the evolutionary relationships occurring in response to weather exigencies.

*B. alba*, an introduced and also indigenous species, may be taken as an example of a birch belonging to the temperate region, and will be used in this investigation because of its intermediate position geographically and structurally, where no special advantage is to be gained by recourse to other species.

OAK.—The oak is the outstanding arboreal form with compound rays. It is this that makes oak wood in great demand for building purposes. The northern oaks show the compound type of ray structure, while on the other hand the southern oaks retain the aggregate type of organization in the mature stem wood. Discoveries of fossil oaks (1, 2) from the gold gravels of California (Miocene) indicate that the aggregate condition was the general one in previous geological epochs. Hence on the basis of comparative anatomy and of geological record the aggregate ray seems to be the primitive one for the oak.

The compound ray was apparently an evolutionary response to the demands of a rigorous winter and to the need of storing up food in abundance. The fact, observable on any hillside in winter, that the oaks of northern latitudes, particularly the seedlings or saplings, retain their leaves late into the winter is an interesting evidence of their southern derivation. The older trees gradually become early deciduous.

Fig. 3 shows a transverse section of a stem of *Quercus rubra*. In the center is a compound ray, composed undoubtedly of homogeneous cells from which vessels and fibers are conspicuously absent. Fig. 4 shows some of these compound rays of the same species in tangential aspect. These may advantageously be compared with the tangential view of the aggregate rays of the birch as shown in fig. 2.

### Birch

WOUNDED STEMS.—Fig. 5 represents the polished disk of a wounded birch log, in which the wound has become so nearly healed that it appears far on the inside of the stem, and would not be discernible from the outside. The return to apparent normal conditions of growth is often very complete in the birch, and bark forms again on the outside. It also occasionally happens that bark grows over wounds of such large extent that the two edges of the injury have not grown together. This region of overgrowth or hypertrophy is known as the wound cap, and is represented at the top of the figure, above the wound. It may be noted in this connection that growth on the side of the stem which has

been wounded has been more rapid than on the lower side where there has been no disturbing influence.

The place in which reversionary structures make their appearance (in this case the aggregate rays) is usually not in the region of the wound nor yet in the wound cap, but in the region of slower growth opposite the wound. This fact will be more apparent when the microscopic features are discussed.

ROOT AND VEGETATIVE STEM OF *B. NIGRA*.—One of the most conservative organs of a plant is the root. Fig. 7 is a transverse section of a root of *B. nigra* showing two rays related to root traces. That these rays are aggregate in organization, and not diffuse, as are the leaf rays of the stem in figs. 1 and 2, may be seen by referring to a still higher magnification of these rays in fig. 8. Taking the root as an organ in which primitive features are long retained after they have been lost in the vegetative axis, it would seem that the aggregate ray is the primitive one for *B. nigra*.

Another conservative region is the node of the stem, and ancestral features are often found here in connection with the leaf ray. Fig. 9 shows a part of such a stem in this critical region in transverse section of *B. nigra*. Although the normal adult stem is characterized by diffuse rays, the aggregate type of organization is present in the first formed annual ring, itself a conservative region.

ROOT, SEEDLING, AND REPRODUCTIVE AXIS OF *B. ALBA*.—Passing from a species with typically diffuse rays, even in the reproductive axis, it is of interest to note the ray organization in significant regions of *B. alba*. As stated, the root which longest retains the older type of ray structure shows such a close resemblance to that of *B. nigra* in important anatomical features that for comparative purposes fig. 7 will illustrate the situation found in the root of *B. alba* sufficiently well. In both the ray organization is aggregate.

Fig. 10 represents a seedling of *B. alba* in transverse aspect, and even under low power the ray structure may be noted as aggregate. A higher magnification to show the detailed organization of one of the rays is not necessary, as they are anatomically similar to that shown in fig. 12 (a leaf ray through the reproductive stem of the same species). Fig. 11 is a low power magnification of a reproductive axis of *B. alba*. Here the decided aggregation of rays in

the foliar segment is a marked feature of the woody cylinder, in connection with contrast with that shown in fig. 9 for *B. nigra*. Fig. 12 shows one of these aggregate rays under a higher magnification.

Since the root, seedling, and reproductive axis of *B. alba* show the presence of aggregate rays, it may be assumed, on the basis of principles derived from the study of living and extinct Gymnosperms, etc., that the aggregate condition is the primitive or ancestral one in these species. This interpretation will be used in the present connection for determining the traumatic responses in wounded stems.

WOUNDED STEMS OF *B. ALBA*.—Fig. 13 represents a transverse section made through a wounded vegetative axis of *B. alba*. The marked acceleration in growth in the wound cap which appears at the top is to be noted, as well as the corresponding retarding on the opposite side. Even under low power the flutings in the annual rings formed after injury may be seen on the side of the stem away from or opposite the wound. These crenulations represent aggregate rays, which are not present in the normal wood, and mark the position where reversionary or traumatic features appear in wounded birch stems. The excessive hypertrophy which is so marked a characteristic of wounded birch stems does not seem to be favorable to reversion, since only diffuse rays are found in the wound cap itself. Fig. 14 is a tangential section through the region opposite the wound of the stem figured in fig. 13. The undoubtedly aggregate nature of the rays is evident. Fig. 15 shows some of these rays under a higher magnification, and the aggregation of rays and fibers is even more apparent.

WOUNDED SEEDLING OF *B. PAPHYRIFERA*.—A species closely allied to *B. alba*, and having the normal wood structure of northern birches is *B. papyrifera*. Fig. 16 represents a transverse view of a wounded seedling of this species. The region where reversionary structures might be expected to occur is opposite the wound (X). Fig. 17 illustrates the condition in the immediate region of the hypertrophy. This is typical of the region of the wound cap in the birches in general. The ray organization in this instance is undoubtedly diffuse, and similar to that shown in the case of the normal stem wood of *B. nigra* (fig. 1).

Fig. 18 is a higher magnification of part of the region indicated by *X*, and is in decided contrast with fig. 17 in ray structure. Here the rays are aggregate in organization at the outer edge of the stem, in that part of the wood laid down after the stem had been wounded. The central part of the stem shows only diffuse rays similar to those in fig. 17. These aggregate rays are true reversions, and the place at which they appear (opposite the wound) is significant for the birches.

WOUNDED SEEDLING OF *B. POPULIFOLIA*.—Since aggregate rays are present as a typical feature of the normal stem wood of *B. populifolia*, it might be expected that they would die out in the region of the wound. This is precisely what does happen. Farther back, laterally, they make their appearance in the cylinder but not as traumatic features.

SUMMARY.—Text fig. 2 represents diagrammatically the ray situation obtaining in the root of *B. alba*, and of the genus as well. In the Betulaceae the aggregate type of ray is found universally in the root, essentially a conservative organ. This ray is in definite relation to the root traces, and is the primitive or ancestral type of ray for the genus.

Text fig. 3 represents a wounded stem of *B. alba*, and shows the comparative acceleration in growth of the wound cap and the rest of the cylinder. No aggregate rays appear in this region of marked hypertrophy. The reversionary structures appear opposite or behind the wound, on either side of the stem, and extend in some instances to the extreme opposite side of the woody axis. The seedling condition is represented in the central part of the figure, the aggregate rays appearing in connection with the foliar segment. The leaf gap is shown in black. The aggregate rays related to the foliar segment persist only through two or three annual rings, and then gradually become diffuse, the diffusion taking place first on the sides of the rays. The reproductive axis is also figured in connection with the foliar segments by supposing that the aggregation does not give way to the diffuse type of ray as in the seedling, but continues aggregate out into the cortex.

CONCLUSIONS.—That the aggregate ray is the primitive one for the birches is borne out by the fact that it is the type of ray



organization that persists in the roots of all species of the genus. The aggregate ray is also found in the reproductive axes of certain species, notably *B. alba*. It appears in the seedling in the mature stem of southern species, and as a result of injury when not normally present in the stem. *B. nigra*, which has diffuse rays in the stem, recalls the aggregate type upon injury to the vegetative axis, and shows an aggregation normally in connection with the root trace. *B. papyrifera*, a northern species, recalls aggregate rays in

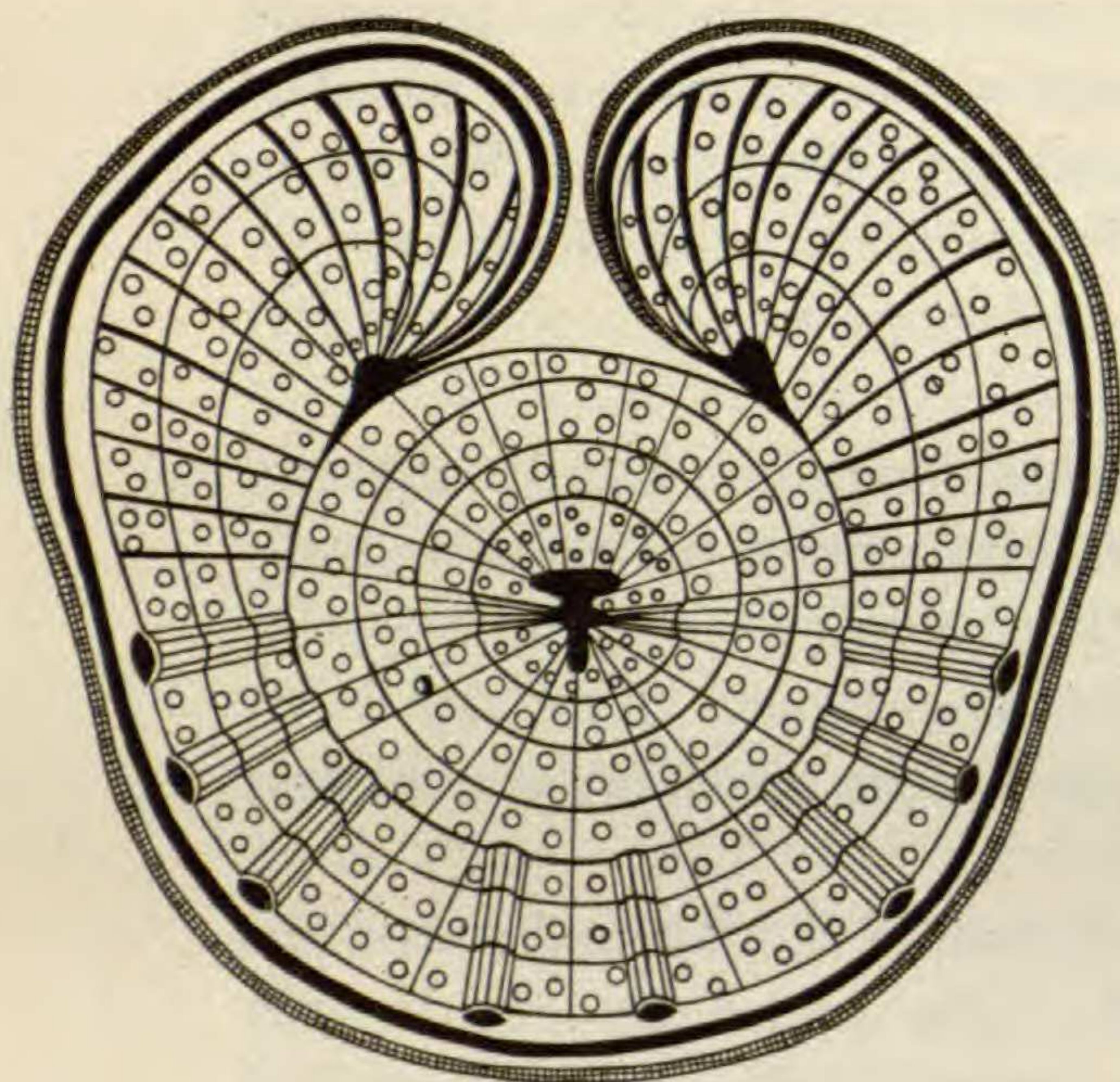


FIG. 3

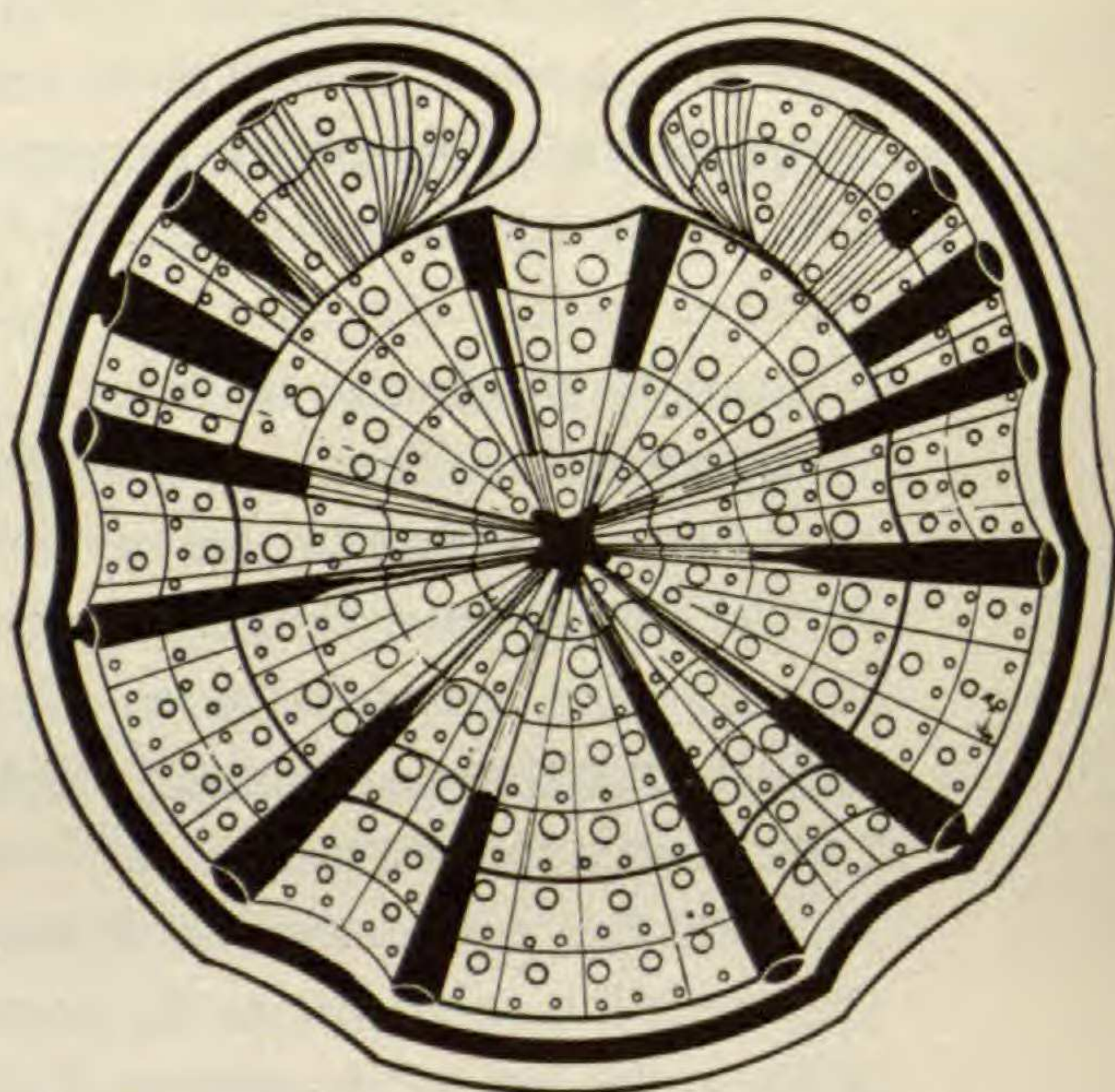


FIG. 4

FIGS. 3, 4.—Fig. 3, diagram of wounded birch stem, showing relations and positions of traumatic features; fig. 4, diagram of oak stem, showing seedling condition and traumatic behavior of ray structures.

the seedling as a consequence of injury. Traumatic reactions should be interpreted in the light of data gained from the organization of conservative regions, etc.

Reactions occurring in the wound cap are the result of hypertrophy and are not to be considered as reversions, since they are not correlated with structures that are known from their distribution in the seedling and conservative regions to be primitive. True reversions in the birch, as exemplified in this investigation by *B. alba* and *B. papyrifera*, occur opposite the wound and not in the wound cap. *B. populifolia*, which has aggregate rays in the

normal wood, loses them as a result of wounding except in connection with the appendage, when they may appear in the wound cap.

### Abies

It will be helpful to summarize the wound reaction situation in Conifers. From the point of view of wound reactions two features are significant, resin canals and ray tracheids. The Abietae show a simplification or reduction of wood organization in lacking both of these characters in the normal wood (3). The root, however, has resin canals as a normal feature of its structure.

In *Abies*, which has neither resin canals nor marginal ray tracheids in the normal stem wood, the situation in regard to reversion is interesting, because both resin canals and ray tracheids are recalled as a result of injury. There is a significant feature, however, in connection with the reappearance of these traumatic characters which parallels the situation obtaining in the angiospermous groups under consideration. It has been pointed out by THOMPSON (8) that marginal ray tracheids which are not normally present in the fir may be recalled as a consequence of injury, and that reversion takes place opposite the wound. JEFFREY (6) had earlier shown that in the case of a wounded stem of *Cunninghamia sinensis* marginal ray tracheids, which are not a feature of normal stem organization, are recalled, and that these make their appearance opposite the wounded region.

The appearance of traumatic resin canals as a result of injury is of special interest from the fact that they do not reappear in the region opposite the wound, as do the marginal tracheids, but in the wound cap itself. This condition, as will be evident later, parallels the situation in *Quercus* in connection with reversionary ray structures.

### Oak

WOUNDED STEMS.—Fig. 6 represents the polished end of a wounded oak log *Q. rubra*. In this instance the healing has not been so complete as it was in the birch, and therefore the wound cap is restricted to the sides of the actual injury. This would be expected as a result of the slow growth of the oak, and accordingly reversionary structures will be expected in the wound cap itself, and

not in the region opposite. Thus it is seen that the place at which reversionary structures occur depends on the localization and nature of the hypertrophy.

ROOT OF *Q. RUBRA*.—The ray structure of the roots of northern oaks is aggregate. Fig. 19 shows a transverse section of a root of *Q. rubra* in which the aggregate nature of the rays is apparent. The details of the aggregation may be seen to better advantage in fig. 20, which represents one of these rays under higher magnification. In the central part of the ray the organization is more parenchymatous than on the outer edges. The aggregate condition persists in the roots of the most mature trees, and is good evidence that the ancestral type of oak ray is aggregate, if it be admitted that the root more than any other organ longest retains primitive features.

Fig. 21 is a tangential section through a root of *Q. rubra*, and the undoubtedly aggregate condition that it presents may be compared with the tangential aspect of ray organization in the stem as represented in fig. 4.

SEEDLING.—The oak seedling in its younger stages has clearly developed aggregate rays. In the older saplings the aggregation may be noted in the first formed annual rings. In the successive annual rings the aggregate type passes over into the compound ray. No separate illustration of this is given because it resembles so nearly that described for the root. Seedlings of *Q. rubra*, *Q. velutina*, and *Q. alba* all show aggregate rays, so it may be assumed that it is a general situation for the genus.

REPRODUCTIVE AXIS.—The reproductive axis of the oak does not show aggregate rays. They have disappeared in the genus probably because there is no longer any definite localization of the acorn-bearing branches, as in the ovuliferous aments of birches. Species of oak of extra-tropical range have in general lost the catkin-bearing habit (in the case of the female flowers).

STEM.—The situation in the oak regarding wounding is somewhat different from that of the birch. The recovery from injury is much slower, and the conditions of atrophy are more marked in the region of the wound than those of hypertrophy. Aggregate rays (1), similar to those figured as normal in the root and seedling,

however, appear in response to a mechanical stimulus, as in the birch.

Fig. 22 represents a transverse section of a wounded stem of *Q. velutina*. The extent of the wound is considerable, and healing has taken place to a comparatively small degree. The wound cap is restricted as a consequence to the edges of the wound, and it is here that reversionary structures make their appearance. The immediate region of the wound cap blots out all large rays, but directly behind this laterally the rays become aggregate, and finally compound again as they approach the back of the stem. Fig. 23 shows some of the rays in the wound cap of fig. 22 under higher magnification. Here the aggregate nature of the rays is quite apparent, especially if it be compared with that showing a typical compound ray (fig. 3). In the immediate vicinity of the wound the rays are all small, and in tangential section appear similar to the diffuse rays of the birch. If one were to interpret conditions here as being reversions, with no reference to the other parts of the stem or to conservative regions, he would have to postulate the diffuse ray as the primitive one for the oak, a situation which is in no wise borne out by the facts of the case, as in neither fossil forms nor in conservative regions of existing species are diffuse rays found. This illustrates the danger of judging traumatic features on their face value without regard to other organs or to the past history of the plant. Only those structures occurring as a result of wounding which can be shown to be characteristic of southern and fossil forms, or of the seedling or conservative regions, can be accepted as significant in connection with wounding in the northern species.

Fig. 24 represents under fairly high magnification a traumatic wood ray of *Q. velutina* in transverse section. It is also illustrative of the manner in which the aggregate ray of the seedling becomes compounded in the older saplings.

It is of interest to note in connection with wound reactions that oak galls produce a return to aggregate condition similar to that ensuing when a stem is wounded in any other way. The organization of the gall itself is complicated, and need not be considered in the present connection.

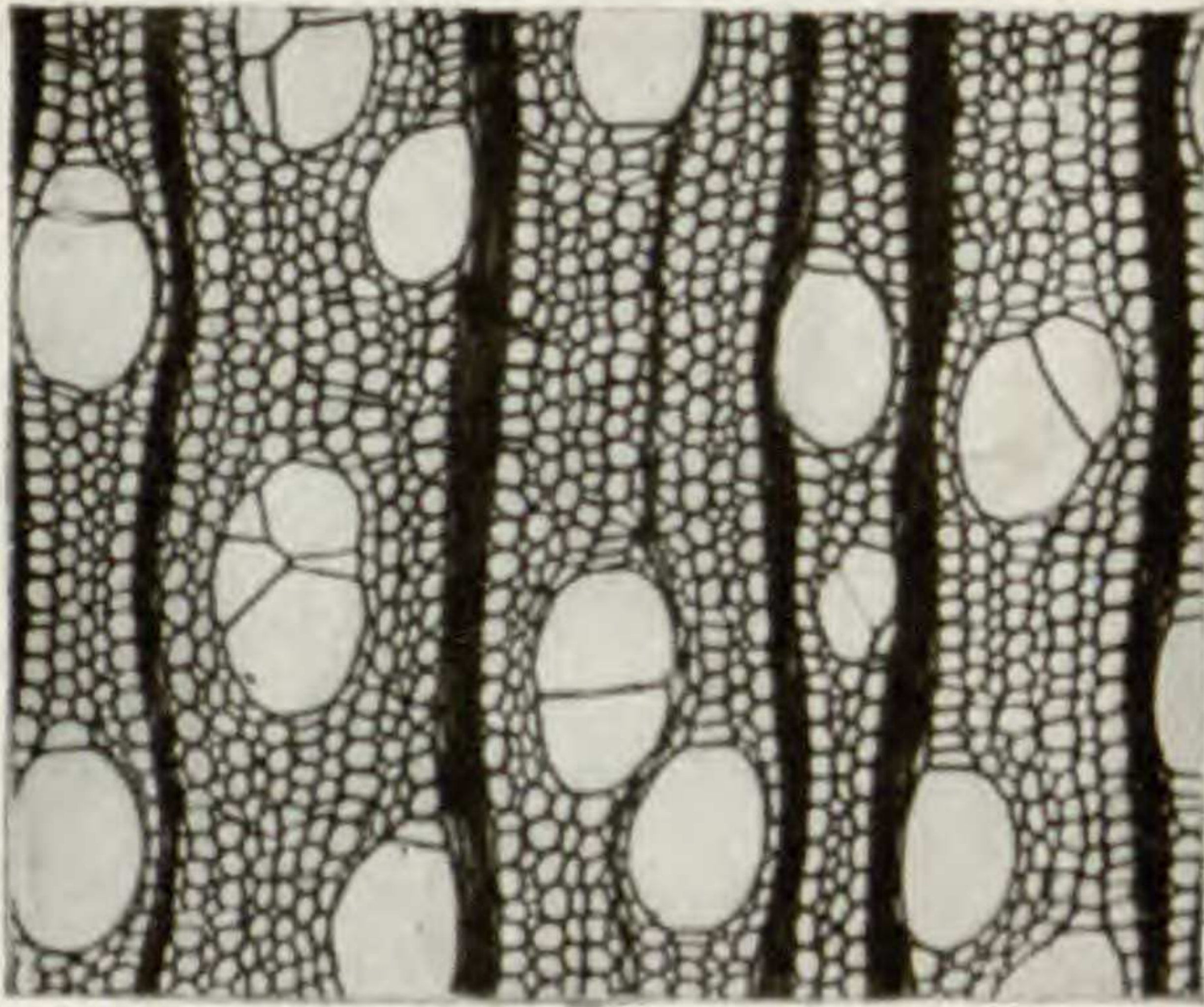
SUMMARY.—The general situation obtaining in seedling oaks and wounded stems may be seen by referring to text fig. 4, which is a schematic representation of a wounded oak stem, and illustrates the position of reversionary features on the edge of the wound cap. These reversionary rays are represented by a series of parallel lines, in contrast with the compound rays, which are solid black. Traumatic aggregate rays occur in the wound cap itself, and laterally they pass over into the normal compound type. A comparison with text fig. 3, representing a wounded birch stem, brings out the important difference in respect to wound reaction and the position of traumatic features in *Betula* and *Quercus*. The transition from aggregate to compound ray in the seedling stem is shown in the center, in which the compound character of the ray is represented in solid black as the ray approaches the periphery of the stem.

CONCLUSIONS.—The northern oaks in their vegetative axes have the compound type of ray typical of the herbaceous forms. On the other hand, the southern oaks have aggregate rays in the adult stem, and fossil representatives of the genus are likewise characterized by the presence of aggregate rays. The seedling and the root of living northern species possess aggregate rays. There is no special localization of the reproductive branches in the oak as in the amentiferous forms like the birch. This region, therefore, which is ordinarily of importance in connection with the determination of primitive structure, is of no value here.

Wounding brings back aggregate rays in the adult axis, and in the older seedlings which have begun to form compound rays. The results of injury here, as in the birch, must be interpreted with reference to the nature and extent of the wound. The wound cap of the oak is much smaller than that of the birch, and does not so often show hypertrophy to any marked extent. Reversionary structures accordingly appear on the edge of the wound in the wound cap proper, slightly behind the immediate region of injury. Oak galls stimulate reversion to an aggregate type of ray structure.

### Summary

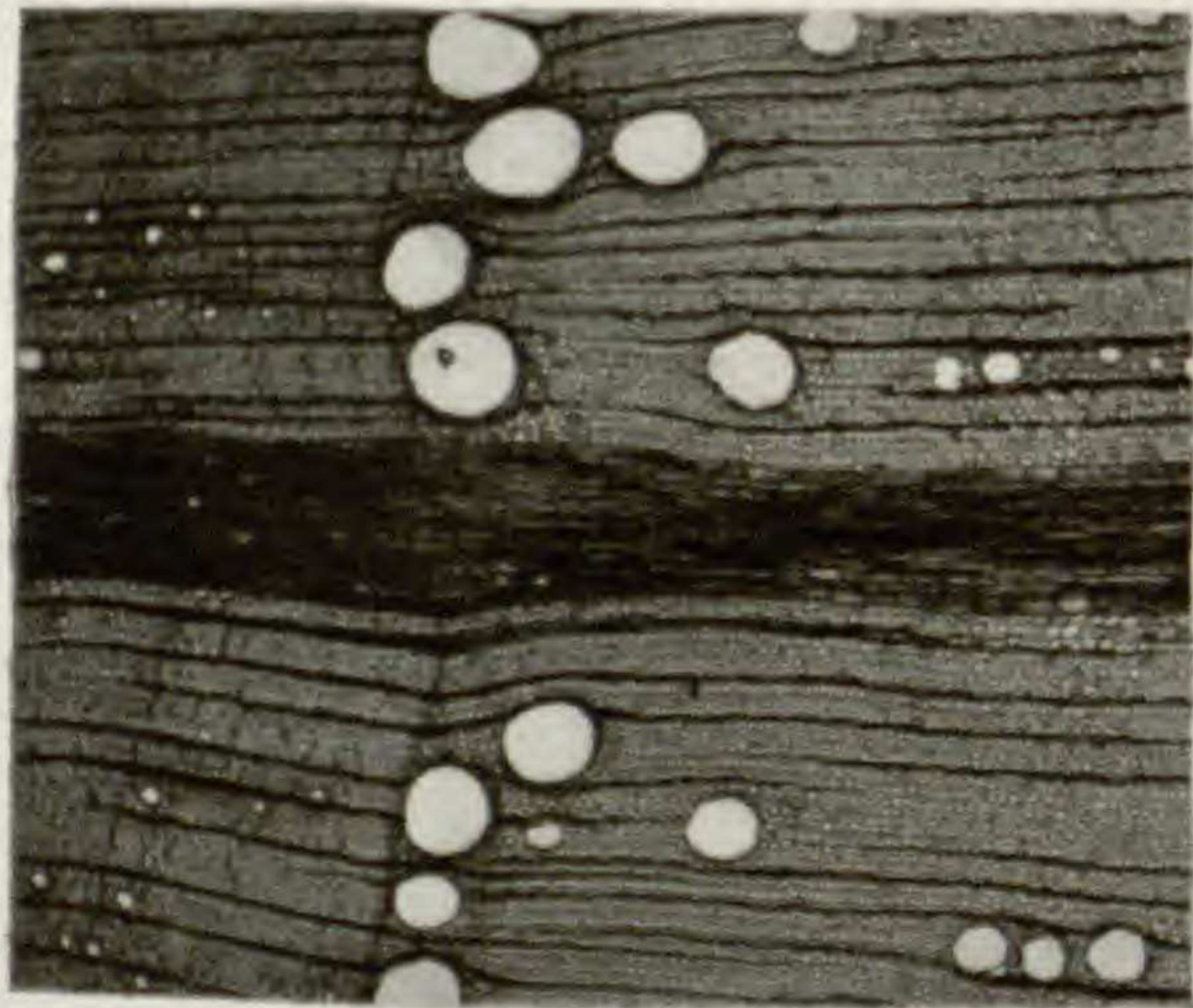
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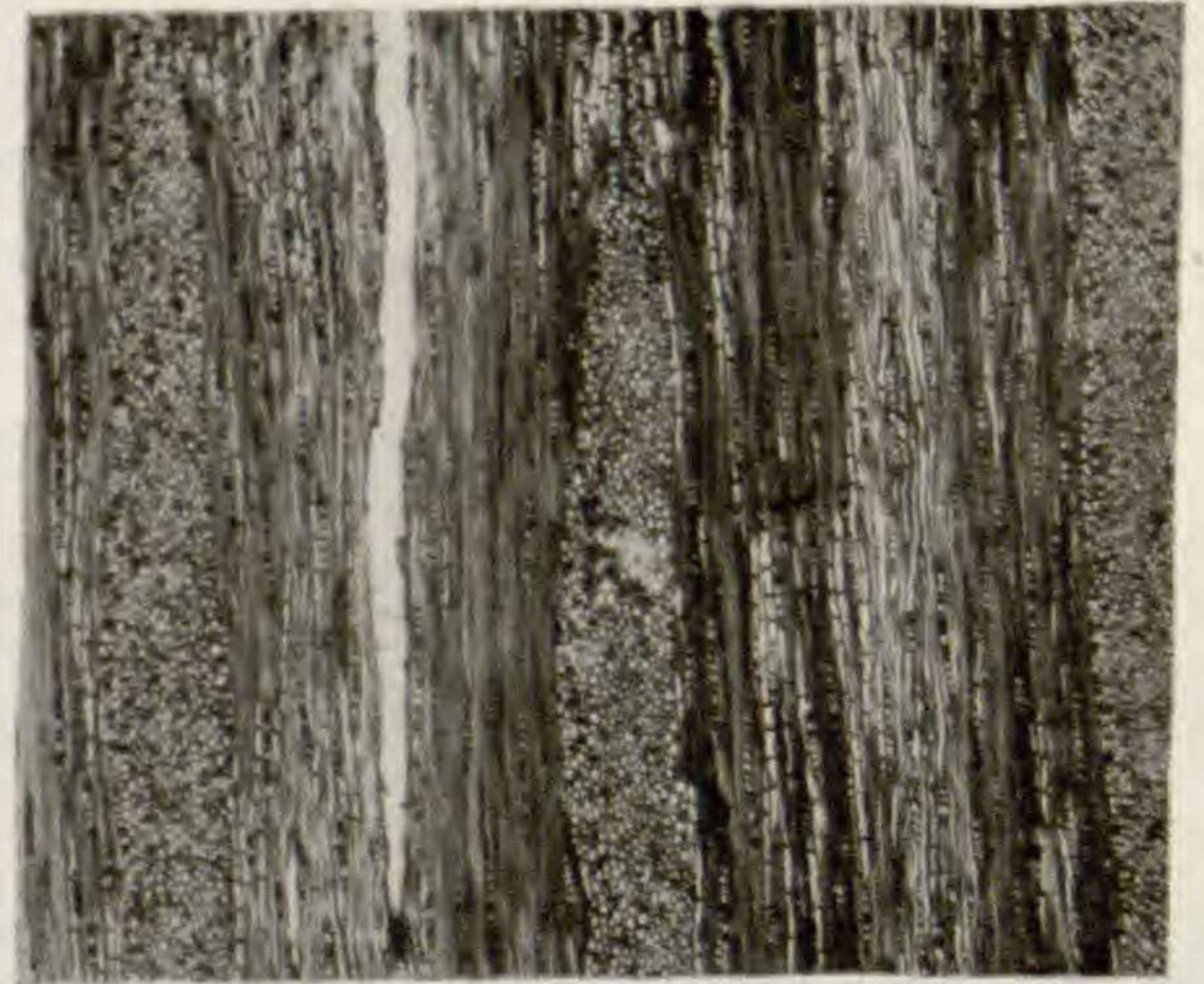
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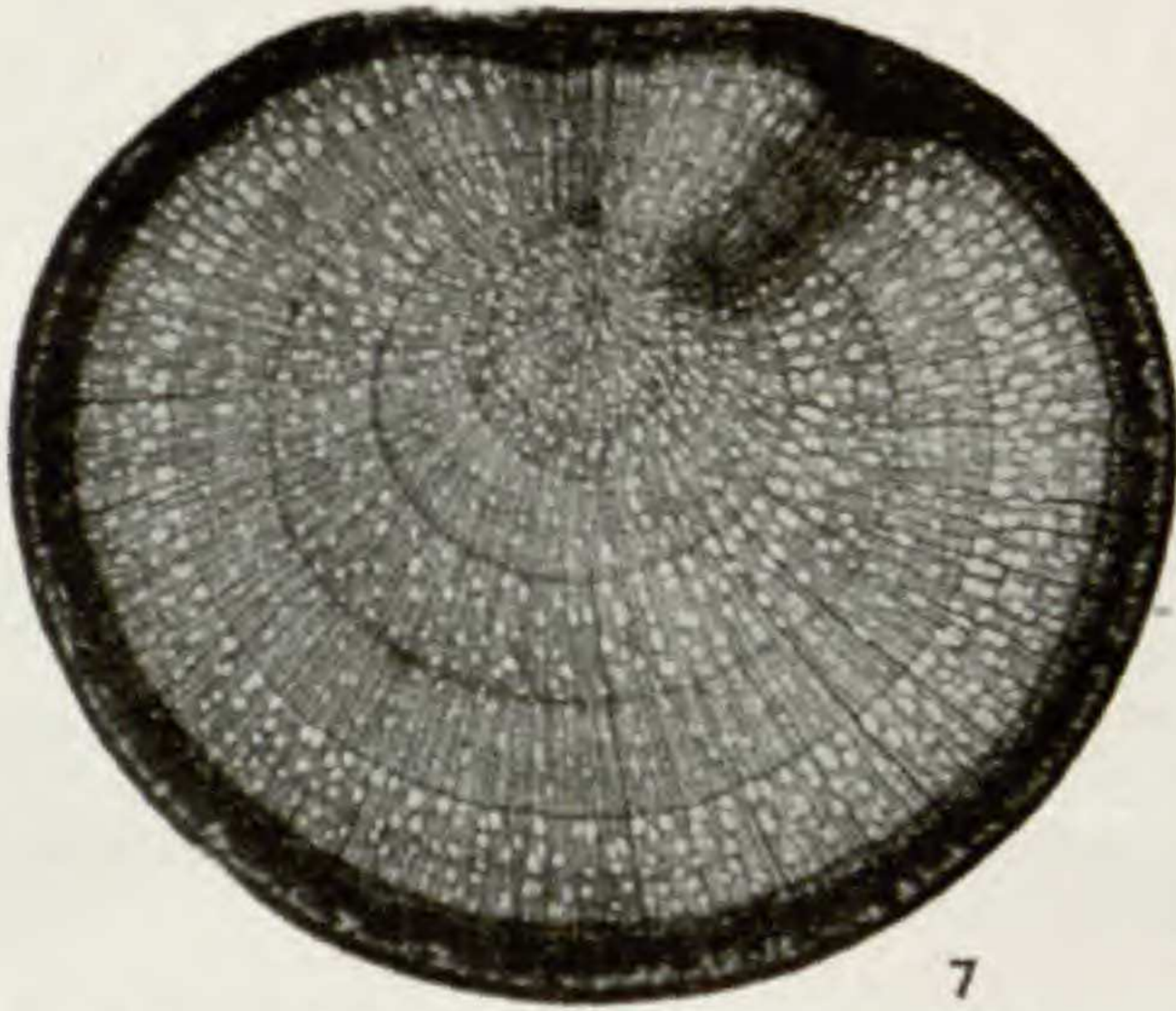


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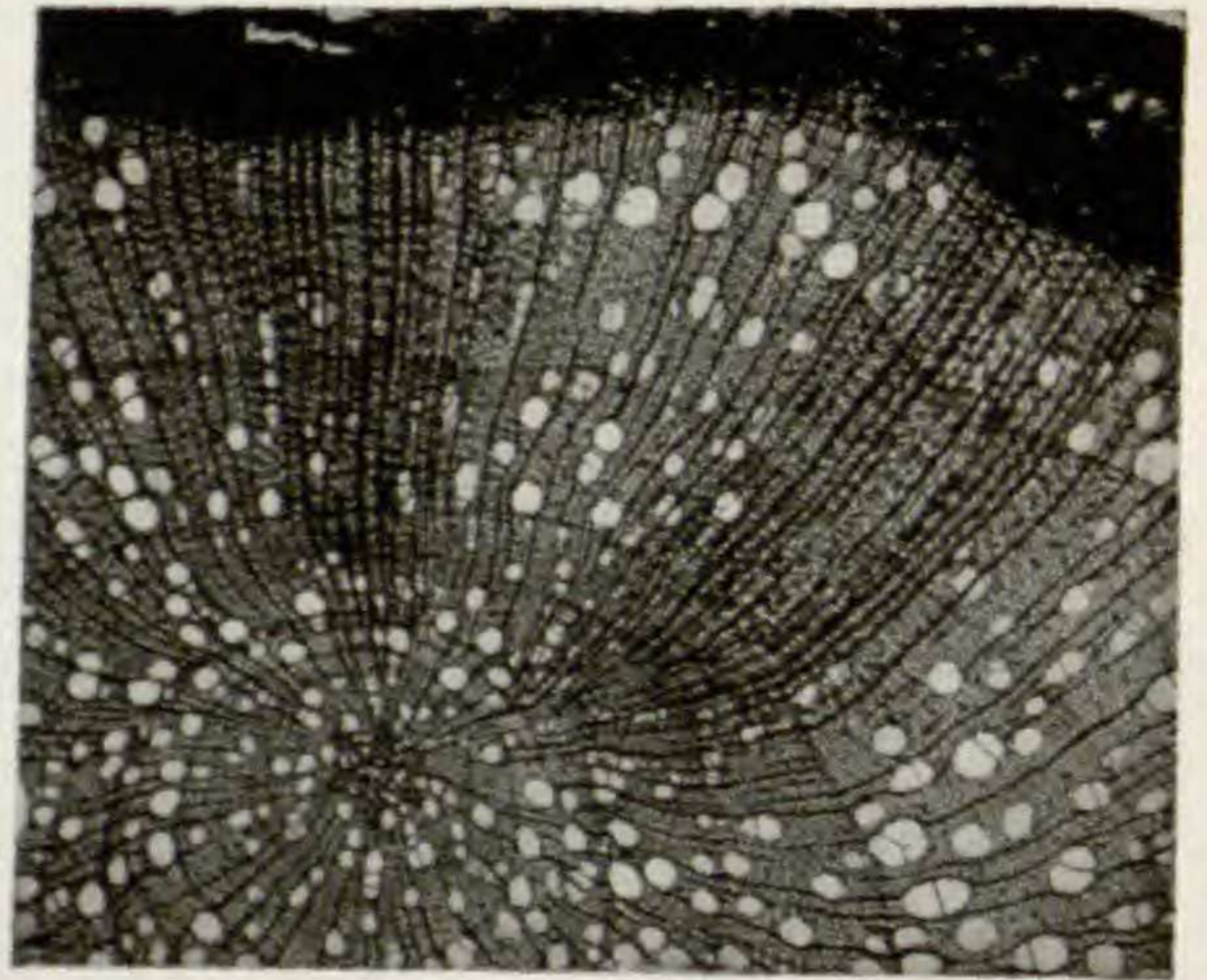


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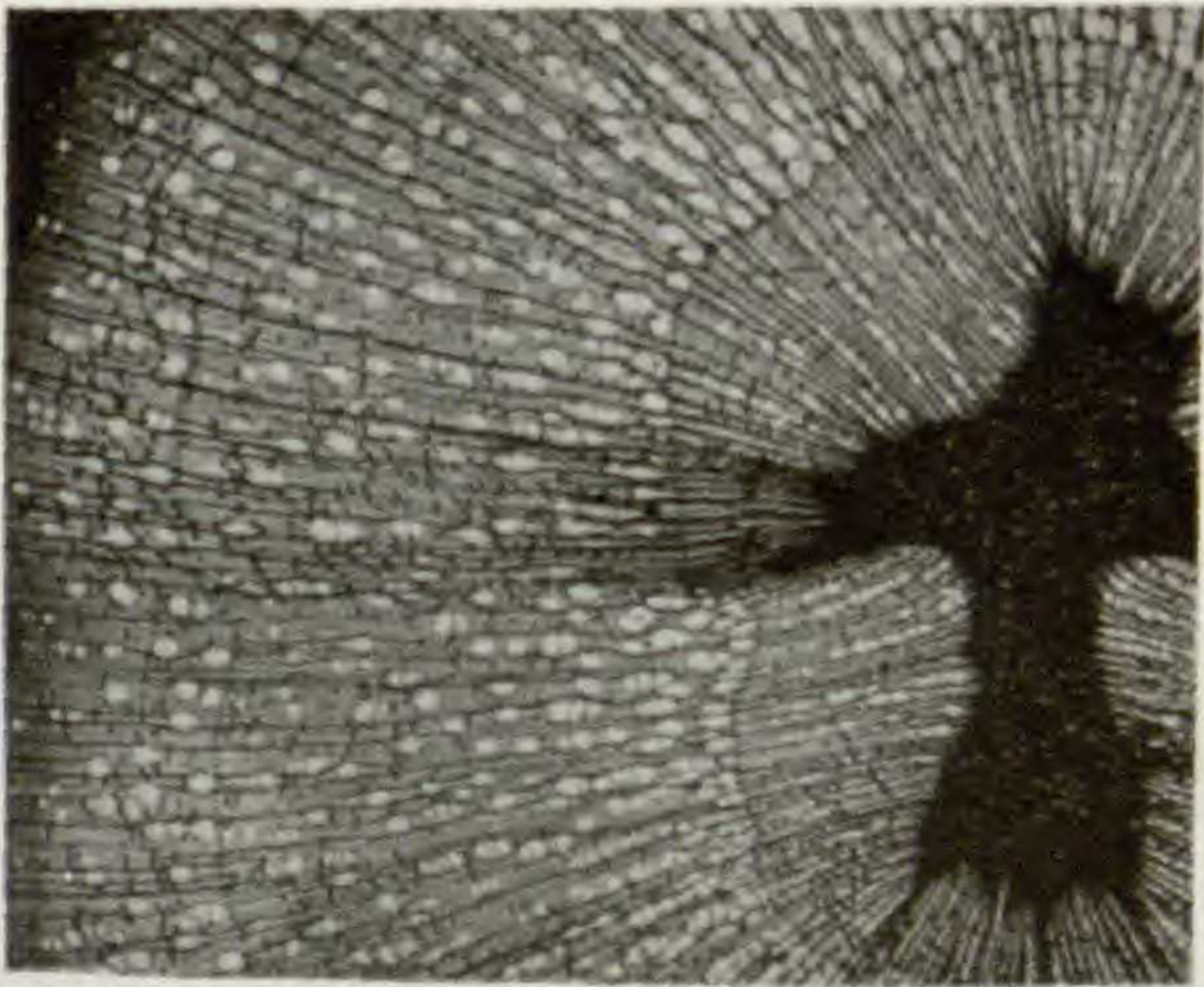
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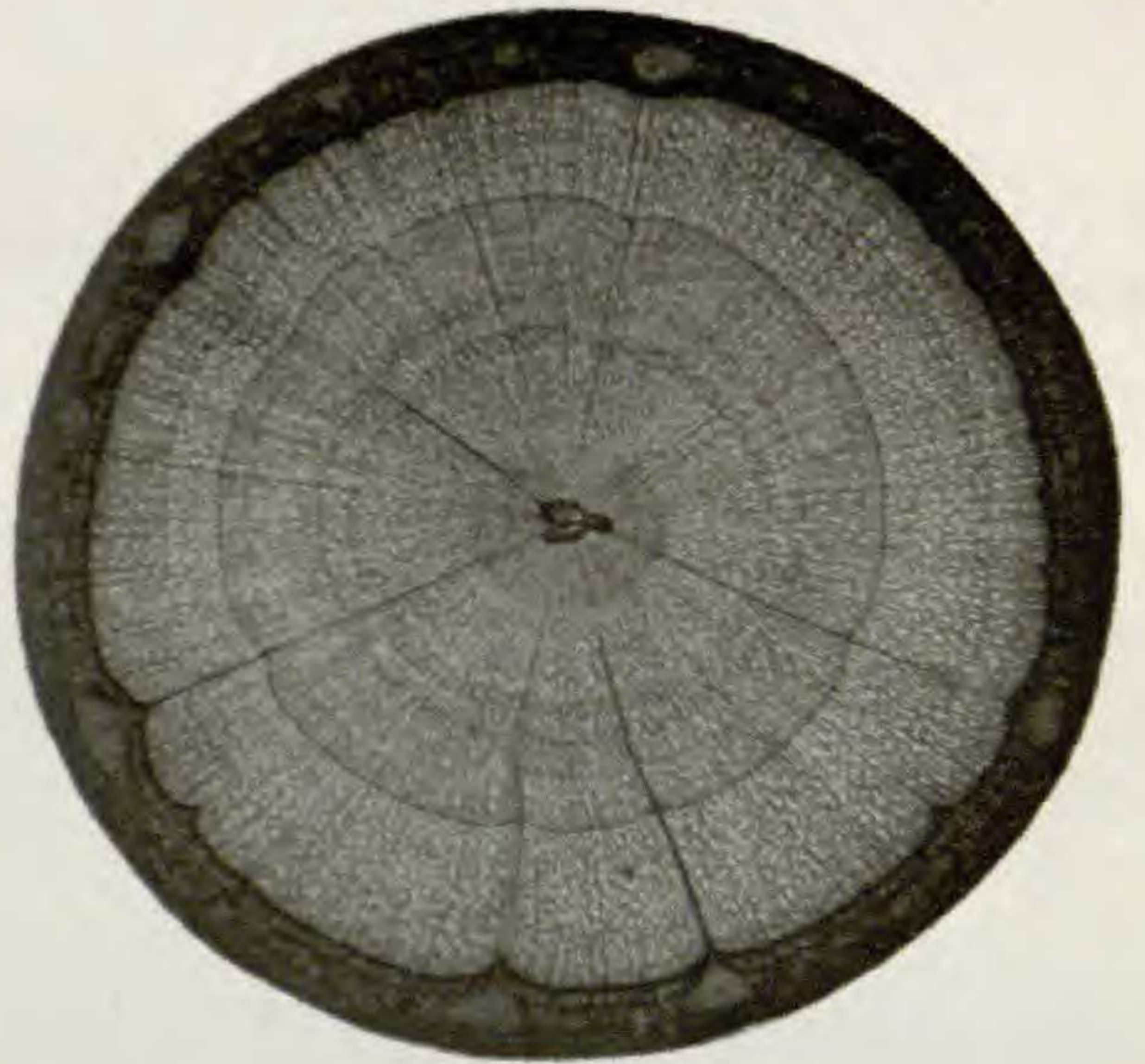
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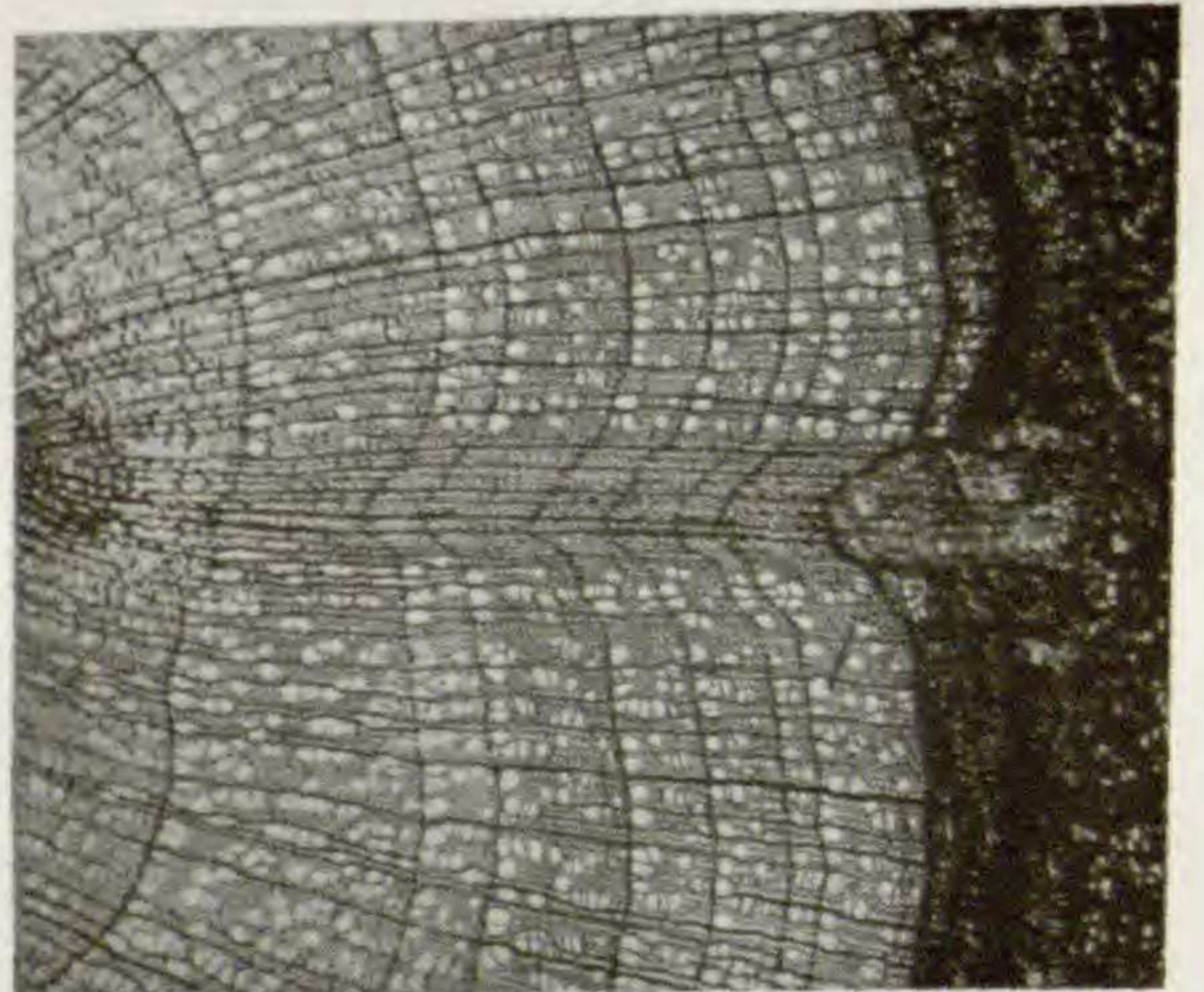
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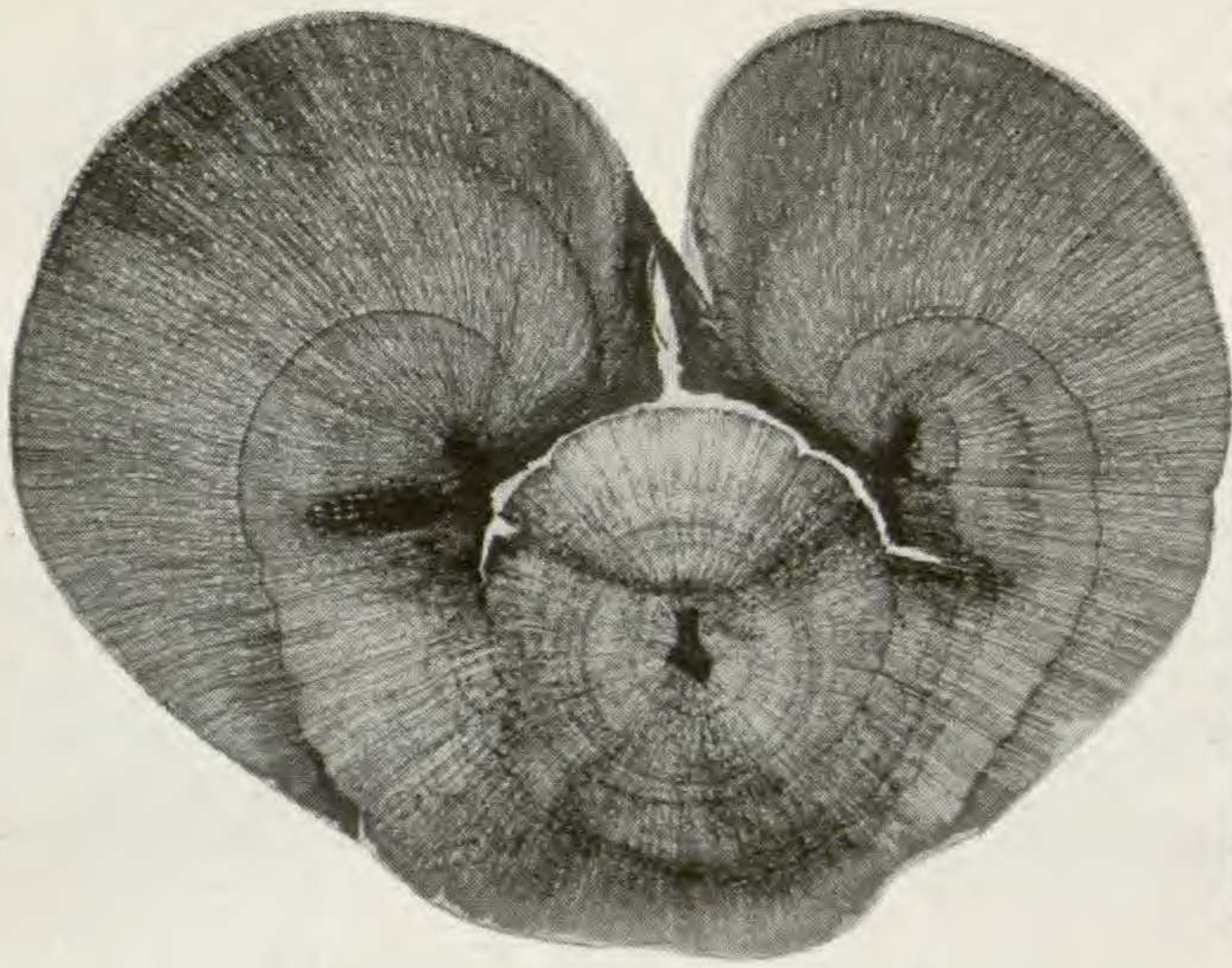


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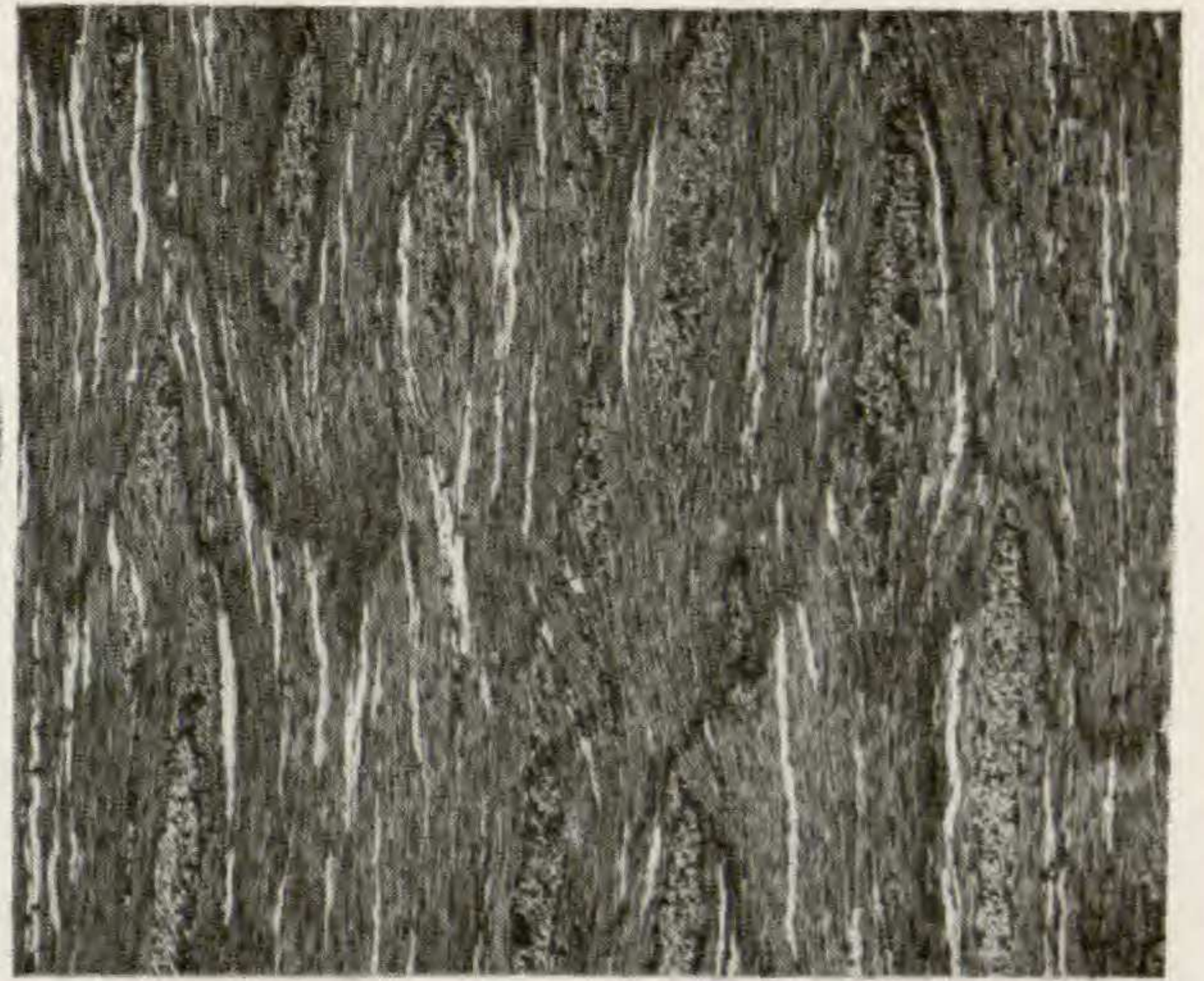


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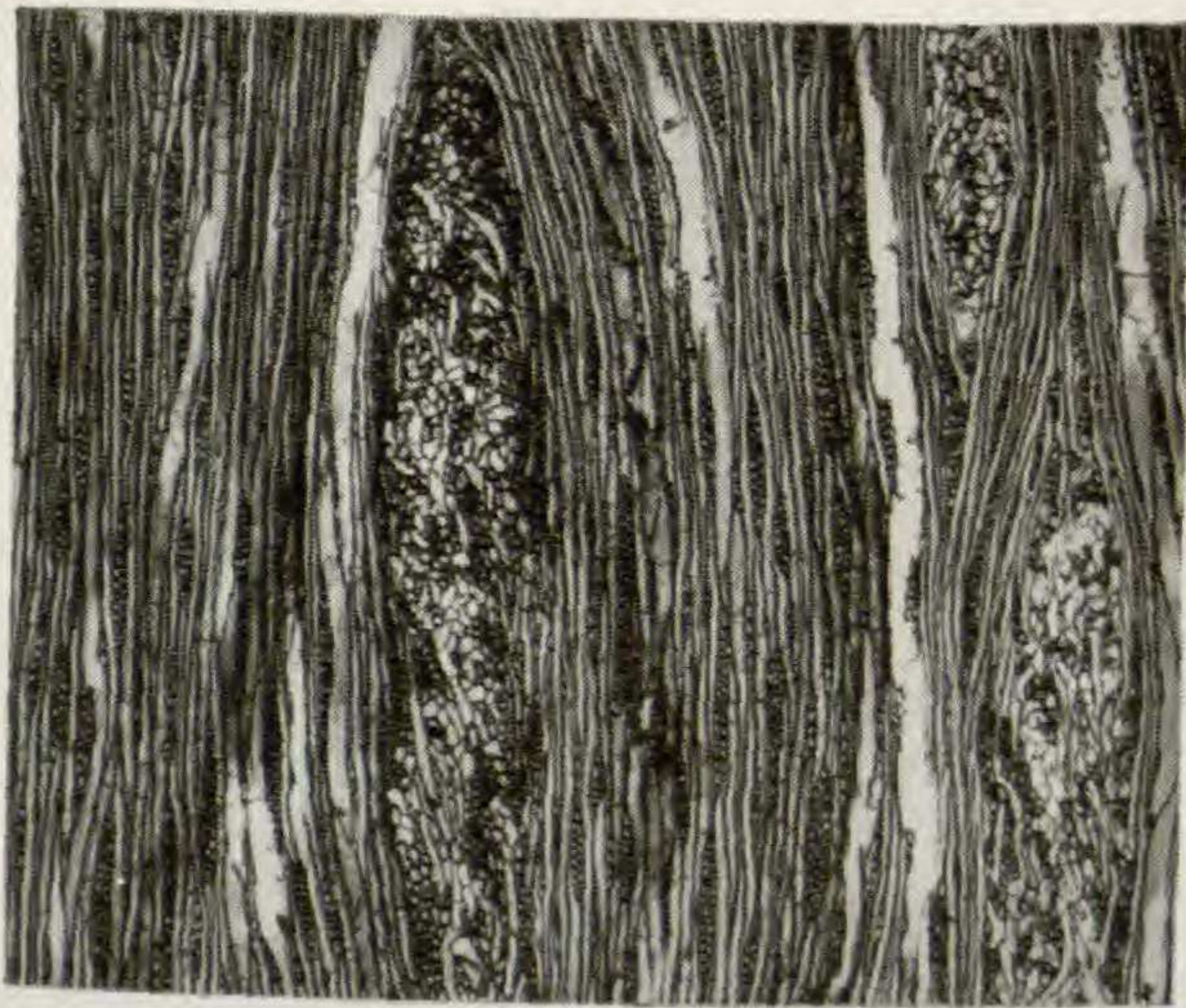
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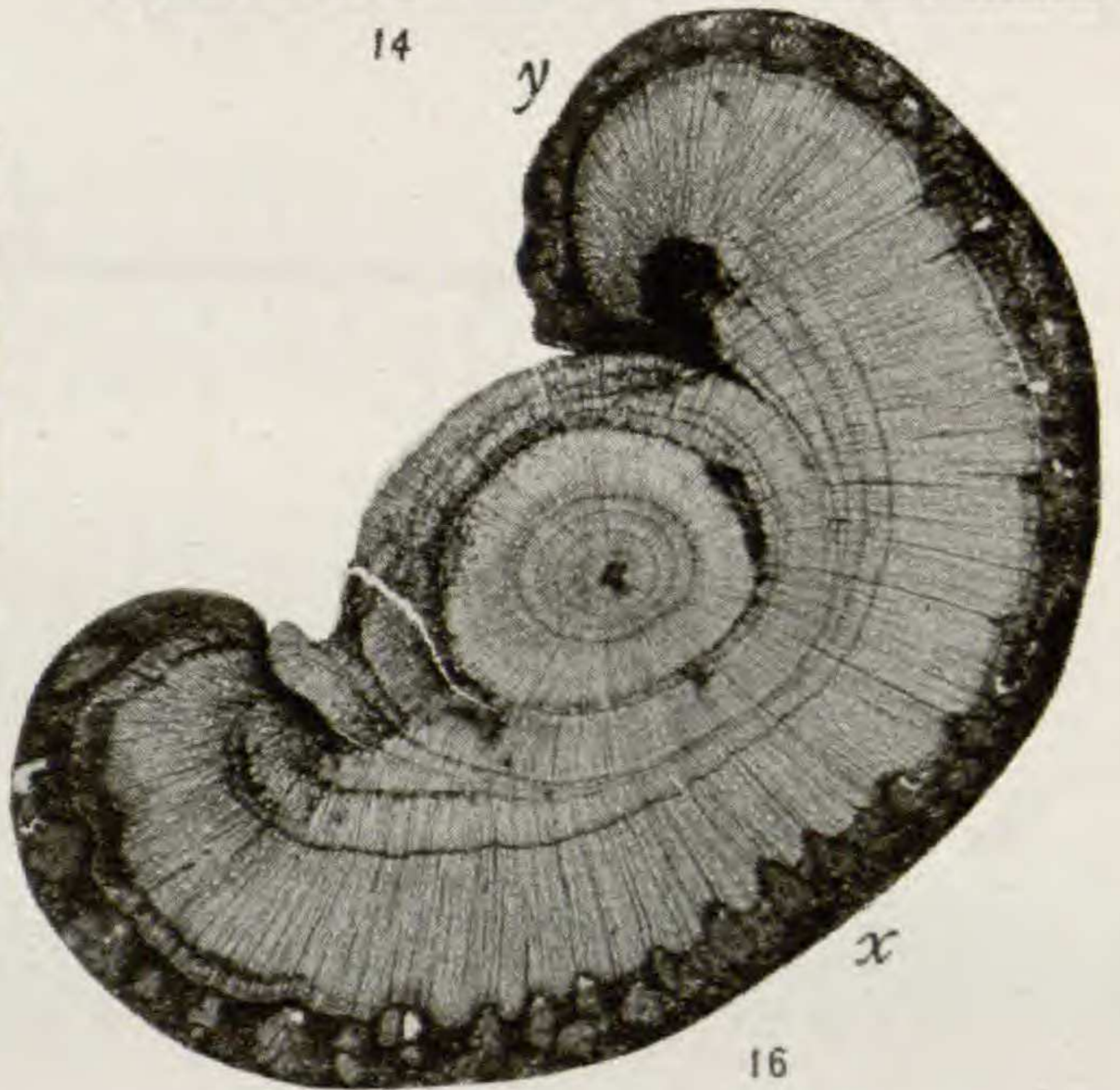
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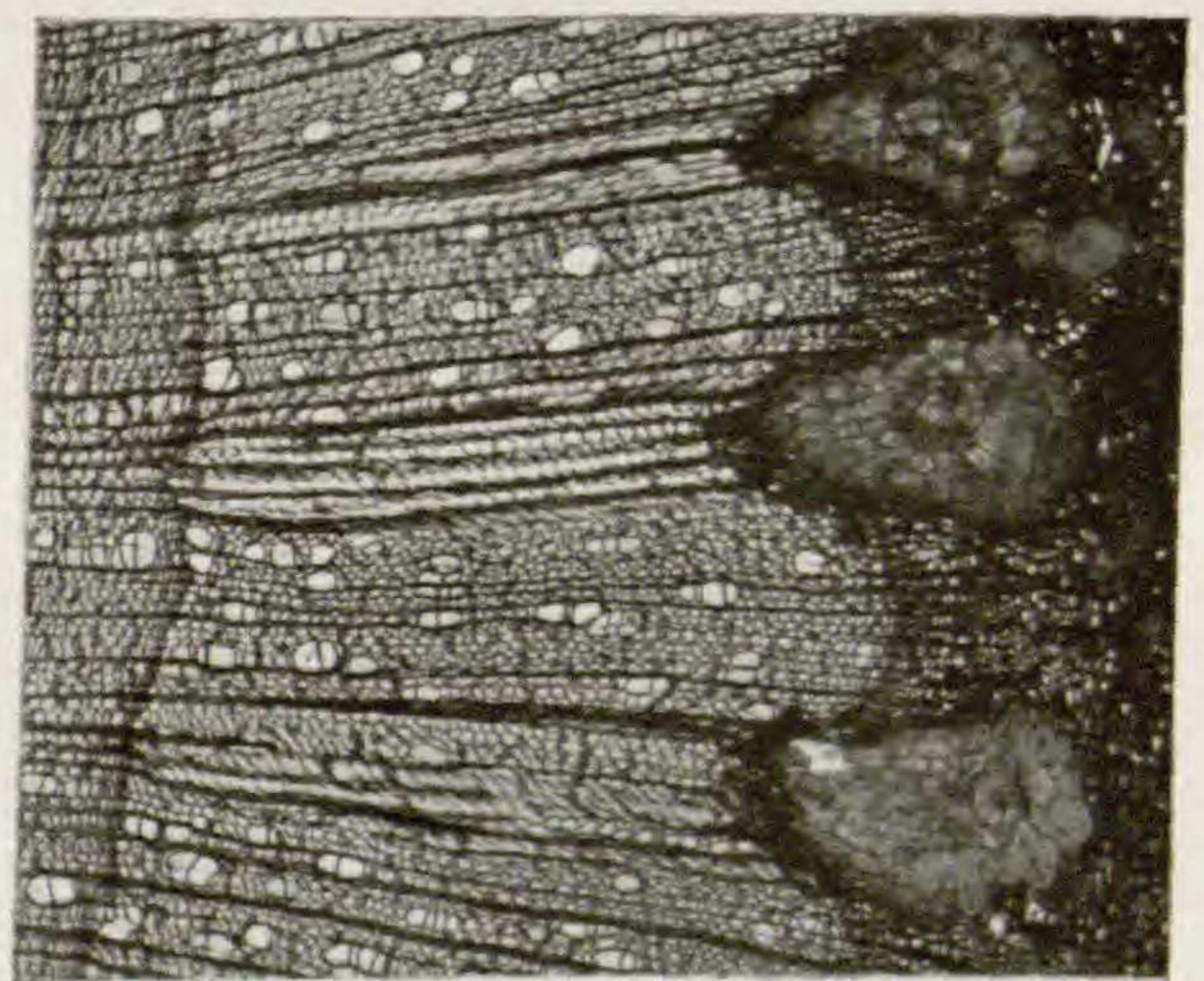


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